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# Biology of snakes of the genus *Tretanorhinus*: an integrative review

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***Abstract.*—Many aspects of the biology of various snake species remain unknown, and the extent of this lack of information is not always clear. As new research usually depends upon previous findings, the gaps in our knowledge and the accuracy of published information are of major importance. Therefore, an analysis of all available information on snakes of the genus *Tretanorhinus*, from both the literature and museum specimens, is presented here to illuminate existing knowledge gaps. The database compiled from 87 documents referring to snakes of this genus and 755 specimens held in scientific collections revealed major gaps and contradictory information for all four species of this genus. Data on morphology, ecology, and natural history are completely absent for *T. mocquardi* and *T. taeniatus*, whereas confusing distribution reports exist for *T. nigroluteus*. The potential consequences of these problems were determined, and some suggestions for correcting them are addressed. Specifically, we consider that focused efforts on the validation of current species and subspecies, field and lab studies of ecology and behavior, and estimations of population dynamics, are necessary.**

**Keywords.** Colubridae, Dipsadidae, ecology, literature review, morphology, museum specimens, natural history, Reptilia, Serpentes, taxonomy

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## Introduction

Fieldwork with snakes usually poses several challenges and more attention has focused on snake species from temperate areas than those from the tropics (Avila et al. 2006), despite the latter having higher diversity (Greene 1997). This bias has resulted in a lack of key information on essential aspects of the ecology, natural history, and behavior of many species. The collection of such data is a time-consuming and difficult task, as many snake species have cryptic habits and occur in low densities (Greene 1997). However, the lack of basic information for many snake species is a major concern, because this information is crucial for making general interspecific comparisons, establishing proper phylogenetic relationships, determining population trends and dynamics, and recognizing differences in behavior. Therefore, reviewing the current state of knowledge for a given species is imperative to identify the areas that require more attention and to guide research and conservation efforts in the proper direction.

Snakes of the genus *Tretanorhinus* are nocturnal, aquatic species that have intrigued biologists for more than a century (Cope 1861; Duméril et al. 1854). Their habits and secretive behavior make them difficult to study, so their biology remains largely unknown (Savage 2002; Schwartz and Henderson 1991). Currently, four species are recognized in the genus: *T. mocquardi* (Bocourt 1891), *T. nigroluteus* (Cope 1861), *T. taeniatus* (Boulenger 1903), and *T. variabilis* (Duméril et al. 1854). Although a handful of studies have increased our knowledge about these species (e.g., Barquero et al. 2005; Dunn 1939; Henderson and Hoevers 1979; Villa 1970), the genus remains poorly studied.

Here we summarize and integrate all available published information, highlight the gaps in our knowledge of the biology of *Tretanorhinus* species, and make suggestions to direct future research in order to fill in these gaps. To achieve this, searches were conducted to find all published material referring directly (i.e., studies focused specifically on one or more *Tretanorhinus* species) or indirectly (i.e., studies focused on many taxa that mentioned one or more *Tretanorhinus* species as part of the topic) to snakes of this genus and a database of key information was compiled (Appendix 1). The information mentioned in each study was used to determine missing data for each species. Each publication was classified using the following categories:

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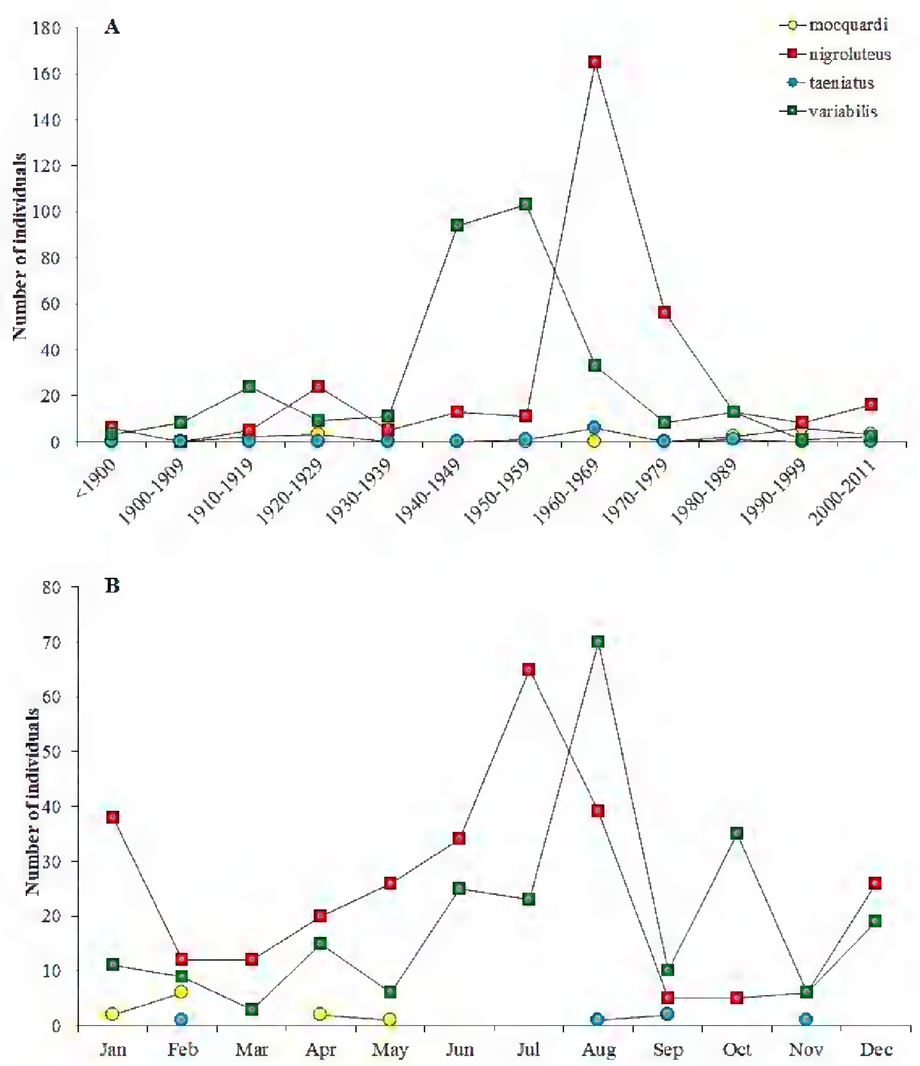


**Fig. 1.** Number of specimens of the four species of *Tretanorhinus* according to **(A)** decade and **(B)** month of collection.

natural history, morphology, taxonomy, systematics, ecology, distribution, biogeography, and reproduction. In addition, data were obtained for specimens held in scientific collections (Appendix 2) from the HerpNet2 data portal (http://www.herpnet.org), Global Biodiversity Information Facility (http://www.gbif.org), Data Research Warehouse Information Network (http://darwin.naturalsciences.be), and by directly contacting collection curators. When available, the following data were extracted: taxonomic classification, type status, sex and age classes, country and locality of the point of capture, latitude and longitude of the collection site, date of collection, and remarks about the individual collected.

## Literature Review and Scientific Collections

The search for publications referring to *Tretanorhinus* produced a total of 87 documents, although only 16 focused directly on species of the genus (Appendix 1). Most of the documents focused on general aspects of natural history (31%), taxonomy (21.8%), and biogeography (20.7%), and the vast majority referred to *T. nigroluteus* or *T. variabilis*, with only a handful of studies mentioning *T. mocquardi* (n = 12) or *T. taeniatus* (n = 8).

A database with information for a total of 755 specimens of *Tretanorhinus* held in 31 scientific collections was compiled (Appendix 2). Most records corresponded to *T. nigroluteus* (n = 350) or *T. variabilis* (n = 357), and only a few were available for *T. mocquardi* (n = 25) or *T. taeniatus* (n = 9). In addition, eight records were identified only to the genus level, and six were mistakenly identified as *Tretanorhinus agassizi*. Most of the collections occurred between the 1940s and 1970s (Fig. 1A) and seasonally between June and August (Fig. 1B), although many records did not include either the year or month of collection.

## Distribution and Habitat

*Tretanorhinus* is a genus exclusive to Middle and South America, and the West Indies. *Tretanorhinus variabilis* is the only one of the species with an unambiguous distribution, inhabiting Cuba, Isla de la Juventud (Isle of Youth), and the Cayman Islands (Fig. 2). *Tretanorhinus nigroluteus* has been frequently recorded along the Atlantic coast from southern Mexico to Colombia, including some islands such as the Bay Islands of Honduras and Great Corn Island of Nicaragua (Fig. 2). However, records of this species in Colombia are controversial. Alarcón-Pardo (1978) reported finding *T. nigroluteus* on the Atlantic coast of Colombia, but we were unable to locate any specimens of this species in the scientific collections consulted which matched the locality mentioned by that author. We found only one specimen of *T. nigroluteus* from the Pacific coast of Colombia as a disjunct point of the species range (Table 1). The distributions of *T. mocquardi* and *T. taeniatus* are the least clear among the species of the genus. *Tretanorhinus mocquardi* ranges from the Canal Zone in Panama through the Pacific coast of Colombia and Ecuador, although it has been reported from only two locations in Colombia and one in Ecuador (Fig. 2, Table 1). *Tretanorhinus taeniatus* could be endemic to Ecuador (Table 1), despite previous reports of this species in Colombia (Castaño-M. et al. 2004; Daniel 1949). Based on these distributions, *T. mocquardi* and *T. taeniatus* could be sympatric in Esmeraldas province, northwestern Ecuador, whereas *T. mocquardi* and *T. nigroluteus* seem to be sympatric in Chocó department on the Pacific coast of Colombia (Fig. 2).

Most information on the preferred habitat of the genus comes from studies conducted on *T. nigroluteus* and *T. variabilis*. *Tretanorhinus* is a fully aquatic genus, inhabiting all kinds of fresh and brackish water bodies such as rivers, streams, lagoons, estuaries, mangroves (Cisneros-Heredia 2005; Neill 1958; Villa 1970), and even cow wells (Seidel and Franz 1994). The species require a muddy or rocky bottom with aquatic vegetation where they can hide and rest (Neill 1965; Villa 1970). Although there are reports of individuals found out of the water (e.g., crossing roads), these events occur after flooding that forces the snakes to search for another water body (Barquero et al. 2005; Villa 1970). The distributions of *T. nigroluteus* and *T. variabilis* also confirm the ability of these snakes to disperse and survive in salt water (Barbour and Amaral 1924; Neill 1958), since they have colonized several islands. In that regard, we observed

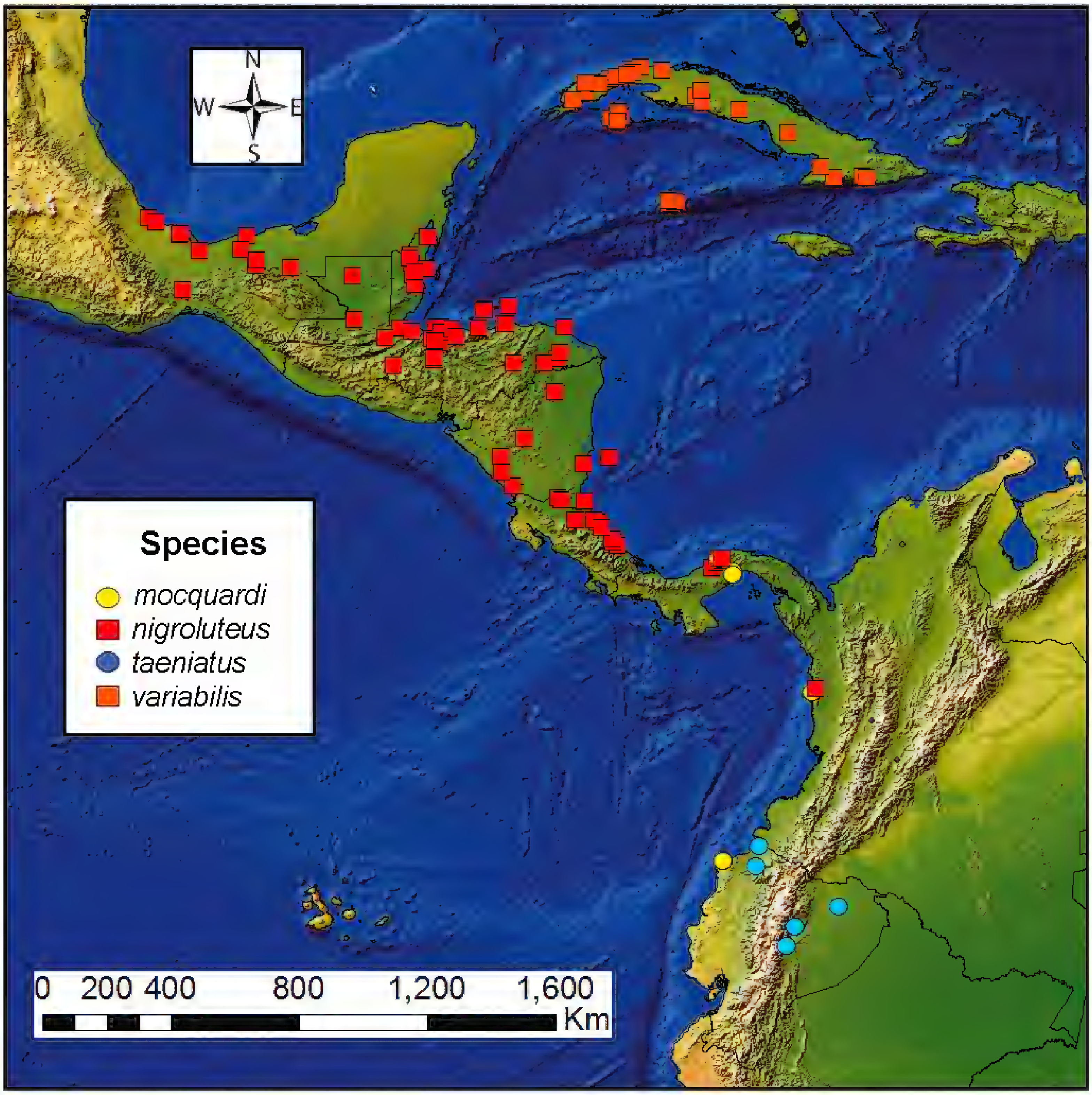


**Fig. 2.** Map showing the current distribution of the four species of *Tretanorhinus* based on specimens from scientific collections.

**Table 1.** Number of specimens of *Tretanorhinus* species collected from different countries and held in several scientific collections. Specimens with a doubtful or missing location were excluded (n = 38).

| Country | *T. mocquardi* | *T. nigroluteus* | *T. taeniatus* | *T. variabilis* | Total |
|---|---|---|---|---|---|
| **West Indies** | | | | | |
| Cayman Islands | - | - | - | 58 | 58 |
| Cuba | - | - | - | 280 | 280 |
| **Middle America** | | | | | |
| Belize | - | 52 | - | - | 52 |
| Costa Rica | - | 11 | - | - | 11 |
| Guatemala | - | 11 | - | - | 11 |
| Honduras | - | 157 | - | - | 157 |
| Mexico | - | 30 | - | - | 30 |
| Nicaragua | - | 65 | - | - | 65 |
| Panama | 14 | 19 | - | - | 33 |
| **South America** | | | | | |
| Colombia | 4 | 1 | - | - | 5 |
| Ecuador | 6 | - | 9 | - | 15 |
| **Total** | **24** | **346** | **9** | **338** | **717** |

**Table 2.** Morphological information available in the literature for each species of *Tretanorhinus*.

| Trait | *T. mocquardi* | *T. nigroluteus* | *T. taeniatus* | *T. variabilis* |
|---|---|---|---|---|
| SVL (mm) | | | | |
| Adults | - | 242–656 | 440 | 500–800 |
| Juveniles | - | 140–168 | - | 143–145 |
| Tail length (mm) | | | | |
| Adults | - | 142–206 | 130 | 145–160 |
| Juveniles | - | 51–77 | - | - |
| No. of loreals | 1 | 1–2 | 1 | 1–3 |
| No. of prefrontals | 1–2 | 2 | 3 | 2 |
| No. of preoculars | 2 | 2–3 | 2 | 1–3 |
| No. of postoculars | - | 2 | 2 | 2 |
| No. of temporals | - | 1+2 | 1+2, 2+3 | 1+2 |
| No. of upper labials | - | 7–9 | 8 | 8–9 |
| No. of lower labials | - | 9–12 | 4–5 | 9–11 |
| No. of ventrals | 166–177 | 127–151 | 168–175 | 152–168 |
| No. of caudals | 69–85 | 56–81 | 74–81 | 48–81 |
| Posterior chin-shields | In contact | In contact | Separated | Separated |
| No. of dorsal rows | 19 | 19, 21 | 21 | 19, 21 |
| Ventral color | Fuliginous yellow | Orange, light red, yellow, cream | - | Bluish gray, dark brown |
| Ventral pattern | - | With or without dots or spots | 3 dark stripes | Light dots or spots |
| Dorsal color | - | Olive, grayish brown, light brown, black | Grayish olive | Grayish olive, dark brown |
| Dorsal pattern | 3 longitudinal stripes | With or without dark spots | 3 longitudinal stripes | Blackish cross bands |

an individual of *T. nigroluteus* resting on a beach on the Caribbean coast of Costa Rica after a heavy rain, suggesting that the snake had been washed out to sea, surviving until it was returned to land by the tide.

## Morphology

Morphological information is limited and incomplete for *T. mocquardi* and *T. taeniatus*, despite both species being described more than 110 yrs ago by Bocourt (1891) and Boulenger (1903), respectively. Table 2 provides a summary of some morphological features that were extracted from the literature review. Overall, *Tretanorhinus* are relatively small snakes; *T. variabilis* is the largest species with an SVL of up to 800 mm. All four species in the genus exhibit a grayish dorsal coloration with stripes, spots, or bands, and a yellow, orange, or gray ventral coloration. Juveniles have been found in the wild only infrequently, and the sex of most collected individuals was not identified (Table 3). Juveniles of each species resemble the adults in pattern and coloration (Barquero et al. 2005; Petzold 1967).

Previous attempts to produce a key to the species of the genus have never included all four species. Therefore, the following key is presented to unify the previous efforts (Bocourt 1891; Boulenger 1893; Dunn 1939; Peters and Orejas-Miranda 1970; Köhler 2008) and incorporate more recent data.

Key to the species of *Tretanorhinus*:

1a. Dorsum without stripes, more than one loreal can be present……………………………………………….2
1b. Dorsum with three longitudinal stripes, only one loreal ……………………………………………………………3
2a. Posterior chin-shields in contact, ventrals fewer than 152……………………………………….*nigroluteus*
2b. Posterior chin-shields separated, ventrals 152 or more………………………………………….*variabilis*
3a. Less than three prefrontals, posterior chin-shields in contact……………………………………….*mocquardi*
3b. Three prefrontals, posterior chin-shields separated ……………………………………………….*taeniatus*

## Taxonomy and Systematics

The evolutionary relationships of the genus are enigmatic and controversial, so that *Tretanorhinus* has been placed within different former subfamilies of Colubridae (e.g., Natricinae, Xenodontinae, and Dipsadinae) by various authors (Crother 1999; Dowling et al. 1996; Pinou and Dowling 1994; Villa 1969). The general consensus is that the genus should be placed within Dipsadidae (formerly Dipsadinae, Grazziotin et al. 2012; Pinou and Dowling 1994) and it is commonly referred to as a xenodontine (Cadle 1985; Minton 1976; Vidal et al. 2000). Moreover, the phylogenetic relationships with other genera are still ambiguous. Crother (1999) placed *Tretanorhinus* as the sister taxon of *Sibon* or the *Sibon-Manolepis* clade. In two studies that included more taxa, Grazziotin et al. (2012) noted that *Tretanorhinus* could be the sister taxon of *Hypsiglena*, and both genera were placed in a clade containing *Trimetopon*, *Geophis*, and *Atractus*; whereas Pyron et al. (2013) placed *Tretanorhinus* as the sister taxon of the *Leptodeira-Imantodes* clade. However, in all these studies the relationships of *Tretanorhinus* with other taxa were poorly supported and the genus is considered as Dipsadidae *incertae sedis* (Grazziotin et al. 2012).

The affinities of each species within *Tretanorhinus* are also enigmatic, and this is caused by the lack of information on the basic biological aspects of some species. Detailed morphological information is only available for *T. nigroluteus* and *T. variabilis* (Table 2). No author has given a complete morphological description of *T. mocquardi*, such that even basic phenotypic traits (e.g., most head scutellation and dorsal coloration) are missing (Table 2). In the case of *T. taeniatus*, morphological information has only been reported for females, as males have never been deposited or identified as such in scientific collections (Table 3). Despite these deficiencies, morphological information compiled from the literature review here suggests that *T. taeniatus* and *T. mocquardi* are more closely related to each other than to *T. nigroluteus* and *T. variabilis*.

Problems have also arisen with the subspecies described for both *T. nigroluteus* (*dichromaticus*, *lateralis*, *mertensi*, *nigroluteus*, and *obscurus*) and *T. variabilis* (*binghami*, *insulaepinorum*, *lewisi*, *variabilis*, and *wagleri*). The morphological variables used to define the subspecies have been chosen arbitrarily (Wilson and Hahn 1973). For example, differences in coloration have been used by some authors to differentiate among subspecies with only superficial descriptions (Schwartz and Ogren 1956; Smith 1965; Villa 1969). In addition, no genetic analyses have yet been reported to confirm the validity of these subspecies.

## Ecology and Natural History

Information on the ecology and natural history of *T. mocquardi* and *T. taeniatus* is virtually non-existent and they remain poorly studied for *T. nigroluteus* and *T. variabilis*. Snakes of *Tretanorhinus* are nocturnal and seem to hide during the day in water bodies amongst roots and rock crevices (Barbour and Ramsden 1919; Stuart 1937; Villa 1970). Some unusual features have been identified for the genus. For example, individuals of *Tretanorhinus* feed upon fishes, tadpoles, and frogs by either actively chasing prey or remaining motionless with the tail and body attached to a supporting surface (e.g., branch or rock) and striking at passing prey (Barquero et al. 2005; Neill 1965; Petzold 1967; Wilson and Hahn 1973). In addition, these snakes demonstrate shy behavior, such as fleeing to the bottom of water bodies when disturbed (Stuart 1937) and rolling up the body like a ball when caught (Petzold 1967; Seidel and Franz 1994). Known natural predators of *Tretanorhinus* include, but are probably not limited to, turtles (e.g., *Kinosternon* [Villa 1973]) and wading birds (e.g., *Tigrissoma* and *Cochlearius* [Villa 1970]). A specimen from Costa Rica was collected from a crab, thus confirming the assumption of Villa (1970) that some species of crabs can be predators of *Tretanorhinus*.

**Table 3.** Number of specimens of *Tretanorhinus* held in scientific collections that have been identified as female, male, or juvenile.

| Species | Female | Male | Juvenile | Total |
|---|---|---|---|---|
| *T. mocquardi* | 2 | 1 | - | 3 |
| *T. nigroluteus* | 14 | 16 | 2 | 32 |
| *T. taeniatus* | 2 | - | - | 2 |
| *T. variabilis* | 19 | 17 | 4 | 40 |
| **Total** | **37** | **34** | **6** | **77** |

Information on reproduction is scarce for all four species of *Tretanorhinus*, although observations in captivity demonstrate that *T. nigroluteus* and *T. variabilis* are oviparous, laying 6–9 adherent eggs out of water (Barquero et al. 2005; Petzold 1967). *Tretanorhinus variabilis* lays larger eggs (35[L] x 16.75[W] mm on average) that hatch earlier (35 d) than *T. nigroluteus* (21.5[L] x 10[W] mm, 42 d). Villa (1970) found gravid females of *T. nigroluteus* during both the dry and wet seasons, suggesting that reproduction could occur year-round in this species. Most gravid females of *T. variabilis* have been found during the wet season in July and August (Petzold 1967; Seidel and Franz 1994). Both *T. nigroluteus* and *T. variabilis* are sexually dimorphic, with females being larger than males and only males possessing tubercles on scales of the head (Henderson and Hoevers 1979; Petzold 1967).

The capacity to survive in salt water likely contributed to the colonization of Caribbean islands and northeastern South America from a Central American ancestor (Cisneros-Heredia 2005; Hedges 1996) and allowed *T. nigroluteus* and *T. variabilis* to become fairly abundant in some parts of their ranges (Henderson and Hoevers 1977; Schwartz and Henderson 1991). Henderson and Hoevers (1977) reported that *T. nigroluteus* was more frequently found during the dry season (December to May) than during the wet season (June to November) of Belize, a difference explained by the overflowing of the river system studied. However, historical collections of this species show that more individuals have been collected during the wet season, a pattern shared with *T. variabilis* (Fig. 1), and in accordance with reports by Wilson and Hahn (1973) for Roatan Island, Honduras. *Tretanorhinus mocquardi* and *T. taeniatus* are less abundant than the other two species and no pattern of variation in abundance can be elucidated from available data.

## General Considerations and Future Research

This study has summarized information about the species of the genus *Tretanorhinus* published from 1854 (Duméril et al. 1854) to the present (Estrella-Morales and Piedra-Castro 2018). Information was also incorporated on all collected specimens of this genus that could be identified as preserved in scientific collections throughout the world. This integrative approach allowed the identification of gaps in our knowledge about these snakes. For example, it is surprising that (1) a complete morphological description is not available in the literature for *T. mocquardi*, (2) only a few specimens have been collected for *T. mocquardi* and *T. taeniatus*, and (3) most natural history and ecological information simply has never been reported for any of the species. In addition to the lack of key data, much available information is contradictory, such as the reported occurrence of *T. nigroluteus* and *T. taeniatus* in Colombia, which can cause several problems. Therefore, one can ask how a reliable identification of individuals in the field can be made when such basic data are missing. This is particularly problematic for sympatric species, such as *T. nigroluteus* and *T. mocquardi* in Panama, and for *T. mocquardi* and *T. taeniatus* in Ecuador.

In order to fill in the gaps in our knowledge of *Tretanorhinus*, future research should focus on at least three areas. First, validation of the currently accepted species and subspecies is absolutely urgent. Barbour and Amaral (1924) have questioned the validity of *T. mocquardi* (although see Dunn 1939), while Wilson and Hahn (1973) refused to recognize *T. n. dichromaticus*. Therefore, a comparative study of all species and subspecies that includes both morphological and genetic data and produces a phylogeny of the genus is necessary. Previous attempts have failed to include all species or have used only morphological or genetic data. Second, both field and lab studies are needed to increase our knowledge about these secretive and, in some areas, elusive species. *Tretanorhinus mocquardi* and *T. taeniatus* require extensive work on morphological variation, ecological habits, distribution patterns, and natural history traits. Breeding behavior is completely unknown for these two species and males of *T. taeniatus* have yet to be measured and described. Although there is significantly more information available for *T. nigroluteus* and *T. variabilis*, nothing is known about their courtship, sexual selection, development, and many other aspects of basic biology. Third, demographic variation and population dynamics need to be quantified to understand the movement of individuals among populations, sex ratios, and population sizes. These types of data are essential for determining the conservation status of species. Some efforts have already been made to identify areas of high and low abundance across the ranges of *T. nigroluteus* and *T. variabilis*. However, long-term studies which monitor changes in populations are yet to be done.

The problems mentioned above are not restricted only to *Tretanorhinus* species, as they also apply to many other snakes (Dorcas and Willson 2009), and it is alarming that we rely so heavily on unconfirmed or erroneous information. Snakes in particular require special attention due to the intrinsic difficulties in generating accurate information. These difficulties arise from certain aspects of their biology, including low densities, great mobility, and cryptic habits. Integrative studies, such as this one, are important for identifying the gaps in our knowledge of different taxa and guiding future efforts in the right direction.

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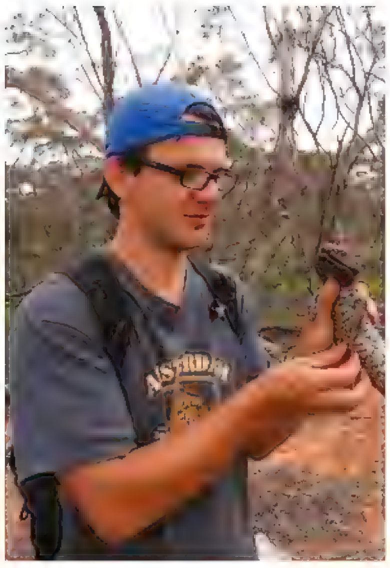

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**Appendix 1.** List of studies referring to *Tretanorhinus* species.

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**Appendix 2**. Number of specimens of *Tretanorhinus* held in each scientific collection from which data were obtained.

| Specimens | Abbrev | Institution name |
|---|---|---|
| 7 | ANSP | Academy of Natural Sciences, Philadelphia |
| 143 | AMNH | American Museum of Natural History |
| 1 | BYU | Bingham Young University, Monte L. Bean Life Science Museum |
| 59 | CAS | California Academy of Sciences |
| 12 | CM | Carnegie Museum of Natural History |
| 2 | CHP | Círculo Herpetológico de Panamá |
| 12 | FMNH | Field Museum of Natural History |
| 82 | FLMNH | Florida Museum of Natural History |
| 6 | FHGO | Fundación Herpetológica Gustavo Orcés |
| 12 | INHS | Illinois Natural History Survey, University of Illinois (formerly University of Illinois Museum of Natural History [UIMNH]) |
| 5 | IBUNAM | Instituto de Biología, Universidad Nacional Autónoma de México |
| 8 | IAvH | Instituto de Investigación de Recursos Biológicos Alexander von Humboldt |
| 35 | LACM | Los Angeles County Museum of Natural History |
| 64 | LSUMZ | Louisiana Museum of Natural History (formerly Louisiana State University, Museum of Zoology) |
| 45 | MPM | Milwaukee Public Museum |
| 15 | MNHN | Muséum National d'Histoire Naturelle |
| 60 | MCZ | Museum of Comparative Zoology, Harvard University |
| 3 | MVZ | Museum of Vertebrate Zoology, University of California at Berkeley |
| 52 | USNM | National Museum of Natural History, Smithsonian Institution (formerly United States National Museum) |
| 11 | BMNH | Natural History Museum (formerly British Museum of Natural History) |
| 5 | RBINS | Royal Belgian Institute of Natural Sciences |
| 3 | ROM | Royal Ontario Museum |
| 3 | TCWC | Texas Cooperative Wildlife Collection |
| 2 | MHUA | Universidad de Antioquia, Museo de Herpetología |
| 12 | MZUCR | Universidad de Costa Rica, Museo de Zoología |
| 2 | UVC | Universidad del Valle |
| 1 | UTCH | Universidad Tecnológica del Chocó |
| 2 | UCM | University of Colorado, Museum of Natural History |
| 77 | KU | University of Kansas, Biodiversity Institute |
| 10 | UMMZ | University of Michigan, Museum of Zoology |
| 4 | UTA | University of Texas at Arlington |
| **755** | **Total** | |